



Compatibility of insect management strategies: *Diuraphis noxia* abundance on susceptible and resistant barley in the presence of parasitoids

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Abstract. Russian wheat aphid, *Diuraphis noxia*, and parasitoid abundance was monitored on field-grown barley, *Hordeum vulgare* L., varying in *D. noxia* susceptibility, to address the applicability of previous laboratory assessments of barley seedling resistance and parasitoid compatibility. Study sites were representative of the barley production region of the High Plains in the western USA, where *D. noxia* and its parasitoids occur. *D. noxia* abundance on resistant barley lines, characterized as partially tolerant and antibiotic to the aphid, was lower than on more susceptible lines. Parasitism by *Diaeretiella rapae*, *Aphelinus albipodus*, and *A. asychis* differed in seasonal occurrence and abundance. *D. rapae* mummies occurred sooner than aphelinid mummies, and there were larger increases in aphelinid mummies than in *D. rapae* mummies during seed head development. But in regard to plant resistance, parasitoid abundance, relative to *D. noxia* abundance, was similar on resistant and susceptible barley lines. Based on the susceptibility of commercial barley to *D. noxia*, the seasonal abundance of *D. noxia* and its parasitoids, and the compatibility of resistant barley and *D. noxia* parasitoids, the use of resistant barley in areas of parasitoid establishment is justified.

Key words: *Aphelinus* spp., *Diaeretiella rapae*, *Hordeum vulgare*, plant resistance, Russian wheat aphid, tritrophic interaction

Introduction

Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) (Homoptera: Aphididae), has adversely affected barley, *Hordeum vulgare* L., productivity in the western USA. Grain yield and quality of commercial cultivars are lowered by *D. noxia* (Webster et al., 1991; Mornhinweg et al., 1994). Insecticides have been used to prevent economic injury (Russian Wheat Aphid Task Force, 1993). However, insecticide use requires higher management and monetary input than occurred before introduction of Russian wheat aphid in this region (Holtzer et al., 1996) and increases risk of

poisoning to wildlife (Flickinger et al., 1991). In recognition of these factors, biological control (Prokrym et al., 1998) and host plant resistance (Webster et al., 1991) management approaches have been pursued.

Biological control activities have documented the presence of *D. noxia* parasitoids in the western USA (Michels and Whitaker-Deerberg, 1993; Elliott et al., 1995; Pike et al., 1997). These include indigenous and introduced strains of *Diaeretiella rapae* M'Intosh (Hymenoptera: Aphidiidae) and introduced *Aphelinus albipodus* Hayat & Fatima and *A. asychis* (Walker) (Hymenoptera: Aphelinidae). *D. rapae* is found throughout the region, but the degree of aphelinid expansion is less known (Elliott et al., 1995; Pike et al., 1997; Brewer et al., 1998a).

Webster et al. (1991, 1993) categorized resistance of nine barley lines as partially tolerant and antibiotic. *D. noxia* feeding on susceptible barley causes leaf rolling and chlorosis, and large populations of *D. noxia* are sustained within curled leaves (Webster et al., 1991). Leaves of resistant barley do not roll, have reduced chlorotic response, and tolerate *D. noxia* presence (Webster et al., 1991). Classification of *D. noxia* resistance has been based on chlorotic and leaf rolling responses of greenhouse-grown seedlings exposed to *D. noxia* (Mornhinweg et al., 1994). Assessment of chlorosis, leaf rolling, and grain yield on field-grown barley were adequately predicted using seedling resistance categories (Mornhinweg et al., 1994; Brewer et al., 1998a).

The potential for incorporation of *D. noxia* resistant traits into commercial barley cultivars raises the question of parasitoid compatibility with resistant barley. The results from previous studies indicated that *D. noxia* resistance in small grain cereals, conferred by several genes, was complemented by *D. noxia* parasitoids under laboratory conditions of artificial infestation of *D. noxia* (Reed et al., 1991; Brewer et al., 1998b; Farid et al., 1998). Plant growth stage, seasonal synchrony of aphid and natural enemy abundance, and abiotic factors in the field may also affect compatibility and may contradict results from laboratory studies (Obrycki and Tauber, 1984). We followed abundance of *D. noxia* and parasitoids on field-grown barley with varying susceptibility to *D. noxia* for the length of the growing season in southeastern Wyoming. The study sites were representative of the High Plains barley production, where *D. noxia* and its parasitoids occur (Brewer et al., 1998a).

Methods and materials

Experimental design. Small plot field experiments were planted to 19 (Laramie, WY, 1993) or 20 (Laramie, WY, 1994 and Wheatland, WY, 1994) barley lines and cultivars. The barley lines and cultivars (referred to as barley lines in text hereafter) varied in *D. noxia* susceptibility and were categorized

as resistant (resistance rating 2: STARS 9301B, R 029, R 023; resistance rating 3: R 022, R 006), moderately resistant (resistance rating 4: MR 019, MR 006, MR 013, MR 009; resistance rating 5: MR 025, S13, MR 001, MR 026), moderately susceptible (resistance rating 6: MS 004, MS 005, MS 003), or susceptible (resistance rating 9: Morex, Robust, B1202, Harrington) (Mornhinweg et al., 1994). The numerical classification system functionally grouped barley susceptibility to *D. noxia* on a scale of 1 (plants expressing no more than small isolated chlorotic spots) to 9 (plants expressing > 85% chlorosis and necrosis with no possible recovery) (Webster et al., 1991). Each barley line was sown in plots measuring 1.52 m by 4 rows spaced 0.30 m apart with a row of resistant barley planted between plots. Sowing occurred in May in Wheatland and June in Laramie, approximately one month later than normal commercial practices to enhance the development of economic *D. noxia* populations. Otherwise, plots were maintained per standard commercial practices (Mornhinweg et al., 1994). The barley lines were replicated four times in a randomized complete block. At Laramie in 1993 and Wheatland in 1994, naturally occurring *D. noxia* populations were supplemented with an artificial release of aphids (approximately 1000 aphids per 0.30 m of row), because there were fewer than 1% infested tillers at the 3-leaf plant growth stage (Zadoks et al., 1974). Within 1 week of infestation, there were more than 10% infested tillers, a typical economic infestation on barley. Plots not exposed to *D. noxia*, by use of an insecticide, were nested within each experiment to assess yield and other plant responses (Mornhinweg et al., 1994; Brewer et al., 1998a).

The USDA-APHIS-PPQ National Biological Control Laboratory (Niles, MI) and University of California (Riverside, CA) supplied *D. rapae*, *A. albipodus*, and *A. asychis* from laboratory cultures reared on *D. noxia* or alternative aphid species (Prokrym et al., 1998) for release adjacent to and surrounding the small plot field experiments. Various strains of each species were released as mummified aphids. Strains were identified by importation code and collection location of the founders of the cultures. *D. rapae* strains released were T92019 (importation code) originating from Wuqia, China and individuals from a combined culture of various strains (Prokrym et al., 1998). *A. albipodus* strains released were T92023 originating from Tacheng, China; EPL92-101 originating from Urumqi, China; and EPL92-56 originating from Pingluo, China. *A. asychis* strains released were EPL92-53 originating from Pingluo, China; EBCL93-24 originating from Xero-Nero, Greece; EBCL93-14 originating from Sicily, Italy; and EBCI93-16 originating from Montmajor, Spain. Two and six releases (approximately 200 individuals per parasitoid species per release) occurred at Laramie in 1993 and Wheatland in 1994, respectively, beginning at the pre-tillering plant

growth stage and continuing weekly. Multiple releases of the same species occurred at the Wheatland site in 1993 before plots were established (approximately 1000 per species). These and other strains were released throughout the western USA, including Wyoming, beginning in 1989 (Prokrym et al., 1998).

Insect abundance data were taken from leaf tillers approximately every 2 weeks for a total of six observation dates. These dates corresponded to the following plant growth stages: seedling growth (25 to 28 days post-planting), tillering (33, 39, or 40 days post-planting), stem elongation (52 or 53 days post-planting), milk stage of seed development (67 days post-planting), dough stage (81 days post-planting), and seed ripening stage (95 or 96 days post-planting) (Zadoks et al., 1974). This allowed comparison of the effects of resistance in barley on insect abundance from the seedling to mature plant stages. Aphids were counted on 10 randomly selected tillers in each plot. Parasitoid abundance was assessed by counting mummified aphids on the same tillers. Shape and color of mummies provided differentiation of parasitism by aphidiids (tan colored mummies with distension of the abdomen) and aphelinids (black mummies with no abdominal distension) (Wraight et al., 1993). On each date, 50% of the mummies, but not exceeding 100, were reared to adults in the laboratory. Species identification was provided or facilitated by the USDA-APHIS-PPQ Biological Control Laboratory (Niles, MI).

Data analyses. Count data per plot were averaged on a tiller basis and transformed by the square root of the count plus 0.5. Data were analyzed separately for each site and year. Our experiments used 19 or 20 barley lines due to interest in comparing seedling resistance to mature plant resistance. In previous research, *D. noxia* resistance throughout plant development was consistent, corresponding to seedling resistance categories (Brewer et al., 1998a). Initial analyses here were designed to confirm the appropriateness of using the parsimonious plant resistance categorization using six resistance ratings. *D. noxia* seasonal abundance was analyzed among barley lines or among lines categorized by resistance rating, disregarding parasitoid presence. An analysis of variance with two interacting factors was considered: plant growth effect was considered using observations taken at six dates, and plant resistance effect was considered using observations taken from 19 or 20 barley lines either analyzed independently or as categorized by six resistance ratings. Included also was the non-interacting blocking factor, given the randomized block design of plots. Here and in subsequent analyses, the resistance and plant growth factors were considered fixed effects; therefore, the residual was used as the error term in significance tests. If the model using

barley lines categorized by resistance ratings explained a greater amount of the total variability than the model using barley lines analyzed independently, then barley lines categorized by resistance ratings were used in subsequent analyses. Using this categorization, orthogonal comparisons may be used to detect trends of *D. noxia* abundance across ordered plant resistance categories as well as plant growth stages (Montgomery, 1991).

Mummy abundance during the last three observation dates, when mummies were readily detected, was considered in an analysis of covariance for each date with plant resistance and the non-interacting blocking effect maintained as factors in the analysis. The two parasitoid types, aphidiids and aphelinids, were treated as multiple covariates (Freund et al., 1986). This analysis allowed estimation of the linear correlation of parasitoid abundance to *D. noxia* abundance (slope), as adjusted for the effect of plant resistance, for each observation date. For both covariates, the slopes were estimated separately by plant resistance category to determine if there were patterns of slope heterogeneity. If such trends were not evident, then slopes were re-estimated, adjusted for the averaged effect across the *D. noxia* resistance categories. The slope estimates of the covariates allowed comparison of the correlation of aphidiid and aphelinid abundance with *D. noxia* abundance during the three observation dates for each site and year. The *t* statistic was used to test whether slope estimates differed significantly from 1.0, indicating a difference in relative population growth of *D. noxia* and its parasitoids (Montgomery, 1991).

Results and discussion

D. noxia abundance. Model explanation of variability for *D. noxia* abundance was increased when barley lines were categorized by resistance ratings. This model better explained total experimental variability (69, 31, and 48% of total variability) than the model using barley lines analyzed independently (22, 6.2, and 8.1% of total variability) at Laramie, 1993; Laramie, 1994; and Wheatland, 1994, respectively. Therefore, the plant resistance categorization was used in subsequent analyses to detect *D. noxia* population trends in the most parsimonious fashion.

D. noxia seasonal abundance differed among barley lines categorized by resistance rating. *D. noxia* abundance on resistant and moderately resistant barley lines (resistance ratings 2, 3, and 4) were lower than on the more susceptible barley lines (resistance ratings 6 and 9) from the seedling through the milk (Wheatland, 67 days post-planting; Figure 1) or dough (Laramie, 81 days post-planting; Figure 2) stages of seed development. This pattern of seasonal *D. noxia* abundance was indicated by a significant plant resistance

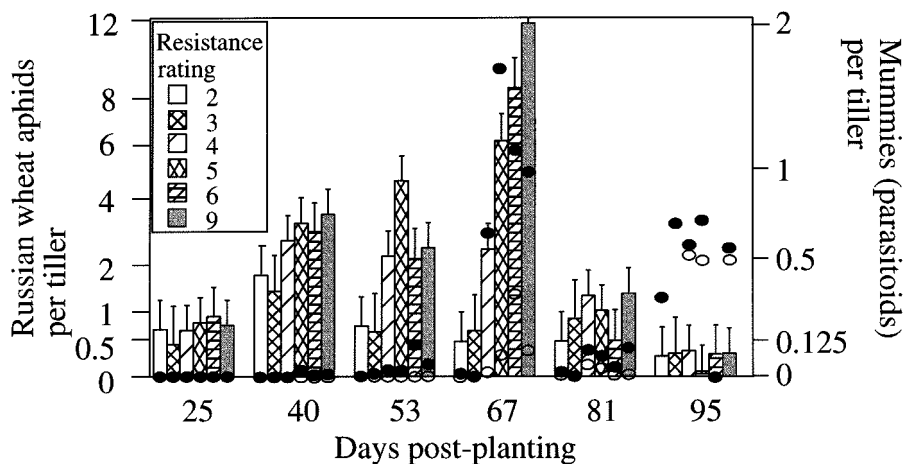


Figure 1. 1994 seasonal *D. noxia* (bars, left axis scale) and parasitoid (open dots indicate aphelinids and closed dots indicate combined aphelinids and *D. rapae*, right axis scale) abundance on barley varying in *D. noxia* susceptibility, Wheatland, WY, USA. Barley lines were categorized as resistant (resistance rating 2, 3), moderately resistant (resistance rating 4, 5), moderately susceptible (resistance rating 6), or susceptible (resistance rating 9). Plant growth stages correspond to days post-planting: seedling growth (25 days post-planting), tillering (40 days), stem elongation (53 days), milk stage of seed development (67 days), dough stage (81 days), and seed ripening stage (95 days). Vertical lines indicate standard errors of means (SEMs). Back-transformed means and SEMs correspond to axes labeled on a density per tiller basis and plotted on the transformed scale.

main effect ($F > 9.4$; $df = 5, 416$ [Laramie, 1993] or 435 [Laramie, 1994 and Wheatland, 1994]; $p < 0.0001$ for the three experiments). After these plant growth stages, *D. noxia* populations decreased in susceptible and some moderately resistant barley (resistance ratings 5, 6, and 9), but were stable or increased for most moderately and all resistant barley (resistance ratings 2, 3, and 4) (Figures 1, 2). A plant resistance by plant growth interaction ($F > 1.9$; $df = 25, 416$ [Laramie, 1993] or 435 [Laramie, 1994 and Wheatland, 1994]; $p < 0.0001$ for the three experiments) signified this pattern. The more susceptible barley lines tended to desiccate sooner than more resistant barley lines, and desiccation generally corresponded to *D. noxia* population decline. But, natural enemy abundance increased during the same period (Figures 1, 2), making suppositions about *D. noxia* population decline difficult. Past field surveys relating *D. noxia* abundance to plant phenology and natural enemy abundance also noted this confounding of factors (Chen and Hopper, 1997).

Relationship of parasitoid and D. noxia abundance. More species were recovered than found in northeastern Colorado surveys conducted before exotic aphelinids and strains of *D. rapae* were released in the High Plains

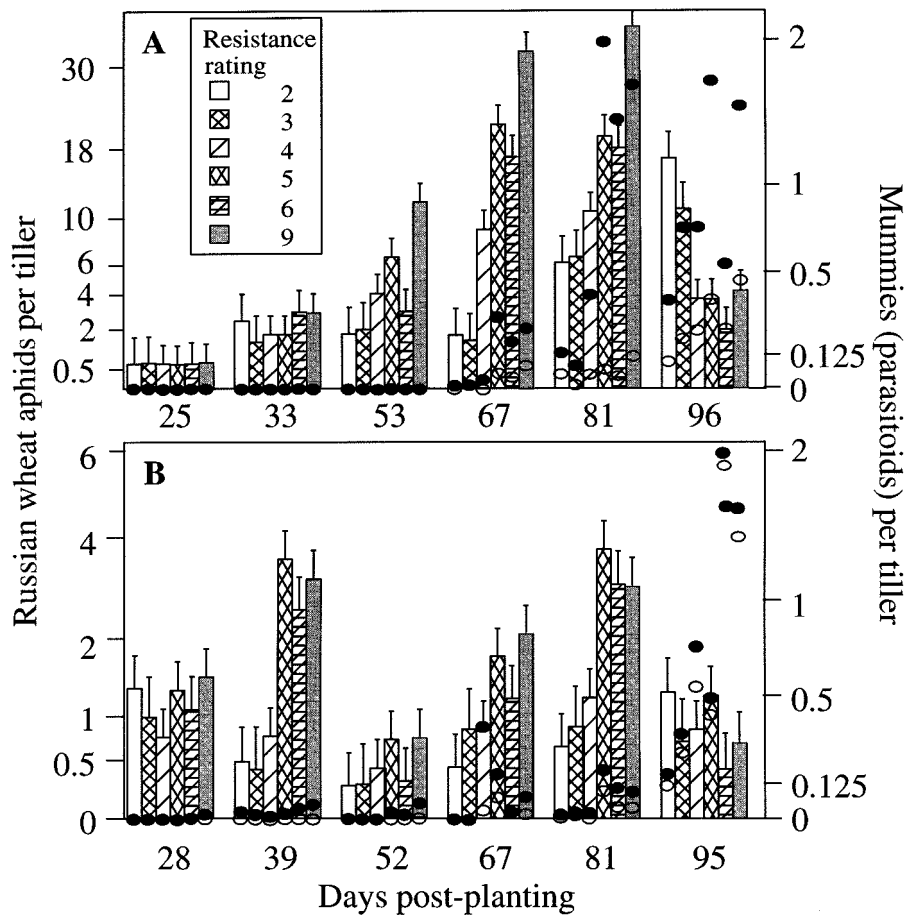


Figure 2. 1993 (A) and 1994 (B) seasonal *D. noxia* (bars, left axis scale) and parasitoid (open dots indicate aphelinids and closed dots indicate combined aphelinids and *D. rapae*, right axis scale) abundance on barley varying in *D. noxia* susceptibility, Laramie, WY, USA. Barley lines were categorized as resistant (resistance rating 2, 3), moderately resistant (resistance rating 4, 5), moderately susceptible (resistance rating 6), or susceptible (resistance rating 9). Plant growth stages correspond to days post-planting: seedling growth (25 or 28 days post-planting), tillering (33 or 39 days), stem elongation (52 or 53 days), milk stage of seed development (67 days), dough stage (81 days), and seed ripening (95 or 96 days). Vertical lines indicate standard errors of means (SEMs). Back-transformed means and SEMs correspond to axes labeled on a density per tiller basis and plotted on the transformed scale. Note change in left axis scale between years.

region. Wraight et al. (1993) identified the primary parasitoids *D. rapae* and *Aphelinus varipes* (Forester) in wheat and barley fields. In our study, *D. rapae* was reared from the aphidiid mummies. The adults emerged from the aphelinid mummies were *A. albipodus* and *A. asychis*. By site and year and averaged over the growing season, species determination indicated 90% *D. rapae* and 10% aphelinids (Laramie, 1993), 60% *D. rapae* and 40% aphelinids (Laramie, 1994), and 80% *D. rapae* and 20% aphelinids (Wheatland, 1994). *A. albipodus* and *A. asychis* occurred in a consistent abundance ratio of 5 to 1, respectively.

Parasitism by *D. rapae* and the aphelinids was correlated with seasonal abundance of *D. noxia*, and parasitoid abundance relative to *D. noxia* abundance was similar on resistant and susceptible barley lines. The covariates representing aphidiids and aphelinids were significant explanatory variables in the analyses of covariance. For the nine analyses (analyses for three observation dates of three experiments), the aphidiid and aphelinid covariates were significant ($p < 0.05$) in eight and seven of the analyses, respectively. Slope heterogeneity among plant resistance categories was seldom detected (covariate heterogeneity representing each of the parasitoid types was insignificant [$p > 0.05$] in seven of nine analyses). Complementing the statistical analyses, parasitoid abundance, relative to *D. noxia* abundance, appeared similar among the barley lines categorized by resistance ratings (Figures 1, 2). Therefore, we report linear correlation estimates of aphidiid and aphelinid abundance with *D. noxia* abundance, as adjusted for averaged effect across the plant resistance categories.

Averaged across plant resistance categories, linear correlations (slope) varied by the two parasitoid types and across plant growth stages (Table 1). There were larger increases in aphelinid mummies than in *D. rapae* mummies late in plant development (Figures 1, 2), as indicated by consistently smaller slope estimates of the aphelinid covariate than the aphidiid covariate during seed ripening (Table 1). During this period, aphelinid populations were increasing as *D. noxia* populations were decreasing (slope estimate significantly less than 1.0; Table 1). Parasitism by *D. rapae* occurred sooner than parasitism by aphelinids (Figures 1, 2), and *D. rapae* abundance was never correlated with lowering *D. noxia* abundance. Slope estimates were never significantly less than 1.0 and at times were significantly greater than 1.0 (Table 1). Seasonal patterns of aphelinid (Chen and Hopper, 1997) and aphidiid (Pike et al., 1997) abundance have been reported from southern France and the Pacific Northwest of the USA, respectively. In our region, there was a much greater mix of these parasitoids, but their seasonal occurrence and abundance was similar to the past surveys. We note that *D. rapae* have been recovered in a broad area of the High Plains, and the

Table 1. Comparison of linear correlations (slope) of aphidiid and aphelinid abundance with *D. noxia* abundance at three plant growth stages, Wheatland and Laramie, WY, USA, 1993 and 1994

Covariate	Plant growth stage (seed development) ^a								
	Milk stage			Dough stage			Seed ripening		
	Slope	SE	<i>t</i> ^b	Slope	SE	<i>t</i> ^b	Slope	SE	<i>t</i> ^b
<i>Wheatland, 1994</i>									
Aphidiid ^c	1.92	0.37	2.50*	2.87	0.73	2.57**	2.21	0.45	2.68*
Aphelinid ^c	1.24	1.11	0.21	3.59	1.85	1.40	−0.11	0.53	−2.07*
<i>Laramie, 1993</i>									
Aphidiid	2.02	1.33	0.77	2.15	0.37	3.10**	0.57	0.31	−1.36
Aphelinid	6.71	3.33	1.71	−1.81	1.98	−1.42	0.44	0.12	−4.57***
<i>Laramie, 1994</i>									
Aphidiid	1.01	0.43	0.02	4.05	1.32	2.31*	1.14	0.43	0.32
Aphelinid	1.27	1.38	0.19	1.60	1.04	0.57	0.60	0.16	−2.51*

The model estimates the slope from an analysis of covariance with the indicated covariates in the model and plant resistance and blocking effects as non-interacting factors.

^a Plant growth stages correspond to days post-planting: milk stage of seed development (67 days), dough stage (81 days), and seed ripening (95 or 96 days).

^b The *t* statistic assesses whether slope estimates differ significantly from 1; * indicates $p < 0.05$, ** indicates $p < 0.01$, *** indicates $p < 0.001$.

^c The aphidiid recovered was *Diaeretiella rapae*, and aphelinids recovered were *Aphelinus albipodus* and *A. asychis* in an abundance ratio of 5 to 1, respectively.

degree of aphelinid expansion from release sites is less known (Michels and Whitaker-Deerberg, 1993; Elliott et al., 1995; Pike et al., 1997; Prokrym et al., 1998).

Related to *D. noxia* regulation, observations from the Laramie site deserve special mention. Parasitoid abundance was approximately equal in Laramie, 1993 and 1994, but *D. noxia* abundance was lower in 1994, never exceeding an average of 4 aphids per tiller (Figure 2). Our augmentation of *D. noxia* and release of parasitoids in Laramie, 1993, was intended to mimic high early-season incidence of *D. noxia* and to establish these parasitoids. Parasitism was common but may have been unable to contribute significantly to *D. noxia* population regulation when early-season infestations exceeded 10% infested tillers. Bernal et al. (1994) found reduced parasitism by *D. rapae* when *D. noxia* densities were increased in a laboratory setting.

Comparison of field and laboratory observations. In choice and no-choice laboratory tests, *D. noxia* on pre-tillering plants of a resistant (STARS 9301B) and susceptible (Morex) barley were parasitized at similar levels by *D. rapae*. *A. albipodus* parasitism was less than *D. rapae* parasitism but did not differ on resistant and susceptible plants (Brewer et al., 1998b). In related work using pre-tillering plants, *D. rapae* and wheat resistance were compatible in regulating *D. noxia* (Reed et al., 1991; Farid et al., 1998). Reed et al. (1991) reported a small degree of enhanced *D. rapae* parasitism of *D. noxia* on uncurled leaves of resistant wheat. Farid et al. (1998) and Brewer et al. (1998b) did not see enhancement nor deterrence of parasitism on several resistant small grain cereals, with *D. noxia* resistance conferred by several different genes.

Even such minor degree of compatibility may magnify the suppression of *D. noxia* on resistant plants, as suggested by Van Emden (1986). The degree of magnification, or depression should resistant plants disrupt parasitoid biology (Read et al., 1970; Van Emden, 1986), may be variable because of shifts in natural enemy response to differences in physical and chemical cues of plants varying in insect susceptibility. In our system, enhanced *D. noxia* mortality by natural enemies on *D. noxia* resistant plants, where leaves do not roll in the presence of *D. noxia*, may be more apparent with relatively large predators, such as coccinellids (Coleoptera: Coccinellidae) than with small parasitoids, such as *A. albipodus* and *D. rapae*. Plants differing in leaf architecture are known to substantially affect the foraging success of ladybird beetles (Farid et al., 1997; Clark and Messina, 1998), but also show little to no effect on *A. albipodus* and *D. rapae* parasitism of *D. noxia* (Brewer et al., 1998b; Faird et al., 1998; Reed et al., 1991). Chemical cues (Read et al., 1970) and the degree of leaf rolling (Reed et al., 1992), particularly in regard to the parasitoids, may be confounding factors.

Our field observations indicated variation of seasonal occurrence and abundance of aphidiids and aphelinids. Corresponding to our field observations, Bernal and Gonzalez (1993) estimated lower developmental thresholds for two species of aphidiids, including *D. rapae*, than for two species of aphelinids. They concluded that aphidiid occurrence in the field would be earlier than aphelinid occurrence, as observed at our field sites (Figures 1, 2). Aphelinid populations increased considerably late in the growing season (Figures 1, 2). This increase may be important in long term *D. noxia* population regulation, if aphelinids are able to utilize *D. noxia* and other aphids found on noncultivated hosts during the summer months when small grain cereals are not in cultivation (Armstrong et al., 1991; Pike et al., 1997). Related to grain yield, *D. noxia* damage to commercial susceptible barley is substantial when low densities occur before seed head develop-

ment (Webster et al., 1991; Brewer et al., 1998a). Therefore, parasitoid–plant resistance compatibility becomes particularly relevant for long-term *D. noxia* population regulation.

In regard to barley resistance, there was good correspondence of laboratory and field observations. Observations of relative aphidiid and aphelinid parasitism of *D. noxia* among resistant and susceptible barley were similar on laboratory-reared pre-tillering plants (Brewer et al., 1998b) and on field-grown plants observed throughout the season (Figures 1, 2). The importance of this correspondence was tempered by the differences in seasonal abundance of the parasitoids. The combination of laboratory and field observations allowed for arguably more rigorous predictions when considering application of tritrophic studies to insect pest management (Obrycki and Tauber, 1984). The interaction of *D. noxia* parasitoids and barley, resistant or susceptible to *D. noxia*, appears more relevant in considering the future potential cultivation of resistant barley and its effect on established parasitoids that may be important in multi-year population regulation of *D. noxia*. Based on the susceptibility of commercial barley to *D. noxia*, the seasonal abundance of *D. noxia* and its parasitoids, and the compatibility of resistant barley and *D. noxia* parasitoids, the use of resistant barley in areas of parasitoid establishment is justified.

Acknowledgements

We thank R. Sinnard and greenhouse staff (University of Wyoming [UW]) for access to and maintenance of field plots at Wheatland and Laramie, respectively. We thank D. Nelson and others (USDA-APHIS-PPQ Biological Control Laboratory, Niles, MI) and M. Waggoner (University of California, Riverside, CA [UCR]) for providing parasitoids and identification services. Among others, we thank D. Gonzalez (UCR), K. Hopper (USDA-ARS Beneficial Insects Introduction Research Laboratory, Newark, DE), F. Gilstrap (Texas A&M University), and members of the USDA-ARS European Biological Control Laboratory (Montpellier, France) for their involvement in making *D. noxia* parasitoids available for release. We thank S. Schanaman, N. Haeffner, P. Yost, and M. Warren (UW) for assistance in data collection. The comments of G. Hein (University of Nebraska), J. Donahue, R. Ahern (UW), and anonymous reviewers of an earlier version are appreciated. This work was financially supported, in part, by a USDA CSREES IPM Implementation Grant (#95-34103-2530), USDA APHIS Western Region contracts, and a cooperative agreement between USDA ARS Plant Science and Water Conservation Laboratory (Stillwater, OK) and UW.

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